

Fruit productivity of Stone pine (*Pinus pinea* L.) along a climatic gradient in Chile



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ABSTRACT

Pinus pinea L. is a Mediterranean species of economic importance due to its edible seeds, the pine nuts that have high market value. We analyzed fruit productivity by recording cone number per tree (CN) on 3464 trees distributed along a climatic gradient in Chile. Cone weight at harvest (CW) and in-shell pine nut number per cone (IS) were measured on 76 superior trees. Climatic and biometeorological variables, defined based on 11 physio-phenological reproductive phases, were related to fruit production traits. Results showed marked differences among North, South and Dry coast areas. The highest values of cone productivity (32 kg tree⁻¹) and CN (62 cones tree⁻¹) were recorded in the South. Stone pine cone production throughout Chile was favored by spring minimum temperature above 7 °C; annual thermal oscillation below 12 °C and late summer temperature below 6 °C during differentiation of reproductive shoots; and a high spring rainfall, except during male flowering period. Accumulated rainfall above 14 mm during 2 year-old conelet growth produced heavier cones. IS significantly increased when accumulated rainfall during cone ripening was above 133 mm. Therefore, water supply would be recommended as a cultural practice to mitigate the negative impact of reduced water availability on fruit productivity.

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1. Introduction

Stone pine (*Pinus pinea* L.) is a well-known Mediterranean species of economic importance; its edible seed, the pine nut, has been used for human consumption since the Paleolithic period due to its high nutritional value (Mutke et al., 2005a). It is characterized by high protein content (more than 32%) and fats (42%), mostly unsaturated, including several mono and poly-unsaturated fatty acids, such as linoleic (omega 6) and alfa-linolenic (omega 3) acids; over 15% of total fiber and low carbohydrate content (Zuleta et al., 2013). Furthermore, protein quality is very high, because it is composed of 20 amino acids (Schröder et al., 2014).

In Chile, the species exhibits vigorous growth and good phytosanitary condition, making its cultivation attractive. Production

is focused on pine nuts due to the high prices they reach on international markets. In fact, pine nuts are among the nine most important dried fruits in the world (Loewe and González, 2007; Soto et al., 2008; Mutke et al., 2005a; Gordo et al., 2011) and have an increasing unsatisfied demand that has stricken the markets in the last decade (Schröder et al., 2014) due to a drastically reduced production (close to 50%) since 2011 (International Nut and Dried Fruits, 2012), which has decreased even more lately.

Stone pine was introduced in Chile by European immigrants; later, early in 1920 it was used in sand dune stabilization programs (Albert, 1909) and in afforestation and rural developments (Loewe and Delard, 2012). Up to 2010, stone pine was established in nearly 100 ha in different regions, settings (isolated trees, groves and plantations) and under different field managements. Those areas have been partially studied for assessing stone pine potential as a fruit tree, confirming its ecological adaptation and productive potential (Loewe et al., 1998; Loewe and González, 2003).

Low levels of the species genetic diversity (Mutke et al., 2012) and remarkable plasticity (Sánchez-Gómez et al., 2009) have been reported, so a high contribution of genotype-by-environment interaction should be expected. Potential cultivation areas in Chile

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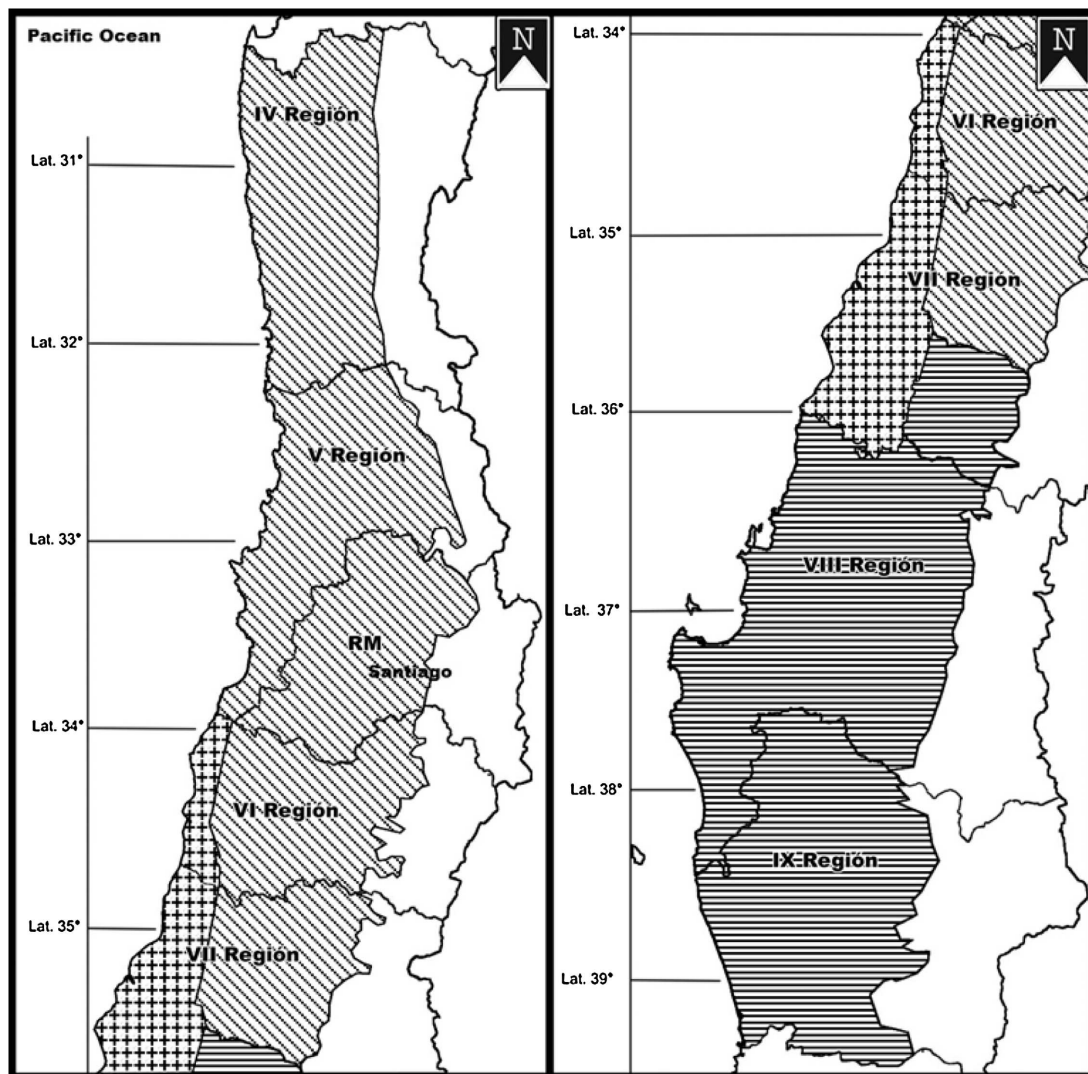


Fig. 1. North (diagonal lines), Dry Coast (squared) and South (horizontal lines) macrozones for stone pine in Chile determined according to stone pine DBH and height growth rates. Total area of each MZ is 5,997,459; 911,351; and 4,596,801 ha, respectively. IV Region: Coquimbo; V Region: Valparaíso; VI Region: O'Higgins; VII Region: Maule; VIII Region: Bio Bio. The Andes Mountain Range runs along the eastern limit of Chile.

were studied by [Ávila et al. \(2012\)](#) considering four categories according to rainfall levels: environmental protection (driest conditions), and low, medium and high fruit production. The authors state that the species can grow in more than 8.6 million ha; of these, over 4.8 million ha are suitable for medium and high fruit productivity. [Loewe et al. \(2015\)](#) determined three macrozones (MZs) according to height and DBH growth rates. South MZ growth rate was superior for height (0.35 m year^{-1}) and DBH ($1.50 \text{ cm year}^{-1}$), whereas in the Dry Coast MZ, the species showed the lowest growth rate in height (0.23 m year^{-1}) and DBH ($0.87 \text{ cm year}^{-1}$).

The species shows a cone production masting habit, which seems to be related to climatic conditions ([Mutke et al., 2006](#); [Calama et al., 2011](#)); this is even more relevant considering that, due to the long fruit cycle duration (3.5 years), a specific climatic event can impact three harvests that are simultaneously present in the tree. In Europe cone production starts when trees are between 10 ([Crawford, 1995](#)) and 20 years old ([Goor and Barney, 1976](#)), but commercial pine nut production involves individuals of about 25 years, with maximum production being attained with 40–50 year-old individuals ([Peruzzi et al., 1998](#)) and being maintained for up to 100 years ([García-Güemes et al., 1997](#)).

Productivity is quite variable over time and regions, and in the main productive countries, it ranges from less than 200 kg ha^{-1} ([Prades et al., 2005](#); [Pinea Project, 2011](#)); between 200 and 600 kg ha^{-1} ([Calama et al., 2005](#); [Centre de la Propietat Forestal, 2009](#)); $600\text{--}1000 \text{ kg ha}^{-1}$ ([Torres et al., 2009](#); [Centre de la Propietat Forestal, 2009](#)); $1000\text{--}5000 \text{ kg ha}^{-1}$ ([Gorrieri, 2010](#); [Mutke, 2011](#)); to over 5000 kg ha^{-1} ([Ottone, 1989](#); [Federlegno-Arredo, 1992](#); [FAO, 1995](#)) in natural forests or plantations with densities ranging between 100 and $400 \text{ trees ha}^{-1}$ ([Borrero, 2004](#)). In Chile, preliminary studies estimated interesting productive levels in plantations, with increasing values up to $70 \text{ cones tree}^{-1}$ in diameter class 41–60 cm ([Loewe and Delard, 2012](#)); however, no study has been performed on variability of fruit productivity along the wide latitudinal range where the species has been planted in the country.

The need to contrast possible environmental correlations with the reproductive biology and phenology of the species has been indicated to identify causal mechanisms for differences in production among populations ([Mutke et al., 2005a](#)), especially considering that environmental factors influence fruit production both in quantity and quality ([Mutke et al., 2005b](#)). For example, in Tunisia, phenology of stone pine plantations was found to depend upon temperature increase in late winter ([Schröder et al., 2014](#)); in

Table 1
Climatic data of stone pine growth macrozones in Chile.

Variable	North MZ (n = 42)	Dry Coast MZ (n = 26)	South MZ (n = 54)	All sites (n = 122)
Annual average temp (AT) (°C)	14.1 (11.8; 16.7)	13.6 (12.5; 15.1)	13.2 (11.0; 14.2)	13.6 (11.0; 16.7)
Annual maximum average temp (MXT) (°C)	21.9 (17.6; 25.1)	21.0 (17.9; 23.0)	19.8 (16.3; 22.5)	20.8 (16.3; 25.1)
Annual minimum average temp (MNT) (°C)	7.5 (5.5; 9.9)	7.0 (5.5; 7.7)	7.5 (5.3; 9.2)	7.4 (5.3; 9.9)
Annual thermal oscillation (TO) (°C)	14.3 (9.2; 17.3)	14.0 (10.7; 17.0)	12.3 (8.2; 15.1)	13.4 (8.2; 17.3)
Annual average rainfall (PP) (mm)	383.7 (116.2; 1260.1)	648.3 (416.3; 816.0)	1,047.0 (523.6; 1666.9)	716.7 (116.2; 1666.9)
Annual hydric index (HI) (mm)	-995.4 (-1349.7; -107.3)	-743.7 (-914.4; -474.2)	-244.1 (-736.4; -332.9)	-628.2 (-349.7; 332.9)
Spring average rainfall (PPsp) (mm)	37.2 (1.5; 143.9)	61.8 (38.4; 89.8)	131.8 (80.8; 218.9)	81.9 (1.5; 218.9)
Spring hydric index (HIsp) (mm)	-394.1 (-483.7; -269.5)	-376.9 (-439.5; -269.9)	-267.7 (-346.4; -121.3)	-337.1 (-483.8; -121.3)
Summer average rainfall (PPsu) (mm)	8.42 (0; 36.4)	29.1 (10.3; 46.3)	58.6 (31.7; 113.0)	33.8 (0.0; 113.0)
Summer hydric index (HIsu) (mm)	-485.8 (-563.1; -328.3)	-460.4 (-571.3; -332.6)	-399.9 (-517.7; -260.5)	-444.1 (-571.3; -260.4)

Values in parentheses correspond to minimal and maximum values recorded for each variable. Hydric index was calculated as accumulated rainfall in the period minus potential evapotranspiration of the same period. n = number of sites.

Source: www.dga.cl.

Table 2
Reproductive cycle of stone pine in central Chile.

Year	Physiologic or phenological phase	Month											
		A	S	O	N	D	J	F	M	A	M	J	J
0	P1. Induction of male primordia												
	P2. Induction of female primordia												
1	P3. Differentiation of reproductive shoots												
	P4. Male flowering												
	P5. Female flowering												
	P6. Pollination												
2	P7. Growth of 2 year-old conelet												
	P8. Growth of 3 year-old cone												
3	P9. Fecundation												
	P10. Embryo development												
	P11. Cone ripening												

Spain, [Abellanas \(1990\)](#) reported a temperature control over stone pine vegetative and reproductive development, with inter-annual differences of up to 20 days and growing degree days (GDD) of those years being similar ([Mutke et al., 2001](#)). Models at different scales have been developed to establish relationships between productivity and several variables ([Cantiani and Scotti, 1988](#); [Cañadas, 2000](#); [Gordo et al., 2001](#); [Piqué, 2003](#); [Madrigal et al., 2009](#)), including climatic ones ([Calama et al., 2011](#)).

Recently, [Loewe et al. \(2015\)](#) determined a climatic impact on stone pine growth across macrozones in Chile. However, these differences could not necessarily be translated to cone productivity; therefore, in order to contribute with knowledge on the dependence of stone pine fruit production upon climatic conditions, we studied this parameter along a 1000 km latitudinal gradient, corresponding to its artificial distribution range in Chile. We aimed to unravel how cone number tree⁻¹ (CN), cone weight at harvest (CW) and in-shell pine nut number per cone (IS) were related to climatic factors across this wide range of environments. We expected to find a lower cone production under drier conditions ([Calama et al., 2008b](#)), thus declining from south to north. The knowledge of this species is reduced in relation to fruit production and one of the strengths of this work is to deepen in the relationships between

fruit production and climatic, as well as biometeorological, variables that relate climate and physio-phenological phases involved in cone induction, formation and development.

2. Material and methods

2.1. Study area and climatic variables

From 2008 to 2013, the Chilean Forest Institute (INFOR) conducted a long-term, large-scale national research effort to gather stone pine data in Chile, covering an area between Coquimbo-IV (30.819817°S) and Araucanía-IX (38.990393°S) regions ([Fig. 1](#)). Inventories of stone pine populations were performed including plantations, windbreaks, groves and isolated trees established for commercial and environmental purposes along the country.

To estimate the potential impact of climate on stone pine cone productivity, several environmental information layers were built based on the Environmental Information Network of Chile.¹

¹ www.dga.cl.

Table 3
Climatic characterization of physiological and phenological phases of stone pine across its distribution area in Chile.

Phase	Average temperature (°C)	Maximum average temperature (°C)	Minimum average temperature (°C)	Rainfall (mm)	Hydric index (mm)	Thermal oscillation (°C)
Induction of male primordia (P1)	17.5 (13.2; 20.9)	25.1 (18.4; 30.0)	10.4 (6.6; 13.3)	44.5 (0; 212.1)	−294.4 (−392.4; −83.7)	5.2 (2.0; 7.4)
Induction of female primordia (P2)	8.9 (6.2; 14.6)	14.1 (10.9; 21.3)	4.5 (0.6; 9.1)	508.9 (0.8; 1,780.5)	386.1 (−143.6; 1691.3)	6.8 (3.1; 10.5)
Differentiation of reproductive shoots (P3)	9.3 (6.6; 14.7)	14.9 (11.8; 22.4)	4.4 (0.2; 8.1)	267.9 (37.4; 898.4)	135.5 (−184.5; 771.2)	6.2 (2.9; 8.6)
Male flowering (P4)	13.3 (10.0; 18.1)	20.4 (14.7; 27.2)	7.0 (3.8; 10.4)	68.1 (0; 272.6)	−167.4 (−298.7; 82.4)	5.5 (1.9; 8.3)
Female flowering (P5)	15.3 (11.4; 20.2)	22.6 (16.4; 28.7)	8.5 (5.3; 12.0)	43.6 (0; 203.1)	−252.1 (−373.6; −42.3)	5.4 (2.4; 10.2)
Pollination (P6)	17.3 (13.5; 21.6)	25.0 (18.5; 31.3)	10.3 (7.2; 13.7)	37.5 (0; 193.3)	−300.4 (−420.2; −58.5)	5.5 (1.8; 8.7)
Growth of 2 year-old conelet (P7)	15.7 (12.0; 19.3)	23.4 (17.7; 28.1)	8.7 (6.1; 12.8)	49.7 (0; 216.8)	−538.6 (−727.7; −231.3)	7.1 (3.8; 12.7)
Growth of 3 year-old cone (P8)	16.3 (12.4; 21.7)	23.8 (18.0; 30.3)	9.5 (5.7; 14.7)	95.7 (0; 323.8)	−651.9 (−955.6; −286.14)	7.8 (2.9; 13.1)
Fecundation (P9)	15.7 (11.6; 19.5)	23.3 (15.8; 28.6)	9.0 (4.8; 12.9)	39.8 (0; 189.9)	−260.1 (−380.7; −113.9)	5.5 (1.7; 10.1)
Embryo development (P10)	17.5 (13.6; 22.2)	26.0 (18.8; 32.2)	10.3 (6.7; 13.8)	56.1 (0; 247.7)	−699.9 (−996.8; −287.4)	7.3 (3.2; 13.4)
Cone ripening (P11)	12.7 (9.8; 18.3)	19.9 (15.2; 25.9)	6.8 (3.8; 11.2)	182.4 (9.5; 661.5)	−37.2 (−290.2; 464.9)	7.5 (3.5; 11.0)

Reported data correspond to average for the phase calculated with all sites. In parentheses, minimum and maximum values of the phase are presented.

Datasets containing relevant environmental predictors were available in a GIS grid format at a resolution of 500 × 500 m and comprised several climatic variables. All environmental variables were resampled according to the WGS 1984-UTM Zone 20S geographical coordinate system at a resolution of ~10 m.

Annual and seasonal (winter, spring, summer and autumn) climatic data were obtained from a 10-year climate series of the meteorological stations that were closest (average distance of 20 km) to the studied sites. If there were several stations available, we selected the most representative one based on topography and bioclimatic areas (Urbe, 2012). The following climatic data were recorded: average temperature (AT); maximum average temperature (MXT); maximum absolute temperature (MXBT); minimum average temperature (MNT); minimum absolute temperature (MNBT) (all temperature variables were calculated on a daily basis and are expressed in degrees Celsius); total annual rainfall (PP, expressed in mm); potential evapotranspiration as defined by Hargreaves and Samani (1985) (PET, expressed in mm); a hydric index (HI) as an indicator of water deficit (HI = Rainfall minus Potential Evapotranspiration, expressed in mm); and thermal oscillation (TO = average maximum absolute temperature minus average minimum absolute temperature for a given period expressed in degrees Celsius).

Table 1 includes the climatic characterization of North, Dry Coast and South macrozones (MZs), as defined by Loewe et al. (2015), and includes annual climatic variables and others related to water availability in spring and summer, because central Chile has a Mediterranean climate, with rainfall concentrated in autumn and winter. Average annual and maximum annual temperatures decrease from north to south; on the other hand, the lowest minimal annual average temperature corresponds to the Dry Coast MZ. Rainfall increases from north to south, whereas the hydric index diminishes, suggesting lowest water deficit in the South MZ (Table 1). The highest variability of climatic variables among sites occurs in the North MZ.

2.2. Stone pine reproductive phases and biometeorological variables

Besides annual and seasonal meteorological variables, we built new climatic variables related to the species reproductive cycle,

named biometeorological variables. These were calculated, for each site and year of measurement, by summarizing the above mentioned climatic variables for 11 reproductive physiological and phenological phases that are important for cone and seed productivity. The 11 phases used in this study were identified from several works (Abellanas and Pardos, 1989; Abellanas, 1990; Mutke et al., 2005a) and adapted to the central area of Chile according to Venegas (2011) and to our field observations (Table 2 and Fig. 2). The reproductive cycle lasts 3.5 years (42 months), and begins in year 0 with the induction of the primordia, first male primordia (P1), then female primordia (P2), in which axillary primordia begin to form secondary cataphylls. In year 1 four phases occur: differentiation of reproductive shoots (P3) when reproductive meristems differentiate in size from vegetative ones, female ones being larger and broader than vegetative ones, with male meristems having an intermediate size; male flowering (P4) when male flowers appear; female flowering (P5) when female strobili appear; and pollination (P6), when mature male flowers open and pollen is released and reaches receptive strobili. During year 2 only one, typically slow phase, occurs, 2 year-old conelet growth (P7). The reproductive cycle finishes in year 3, with four phases: 3 year-old cone growth (P8), when cone and seeds develop; fecundation (P9), in which the pollen tube is formed and fertilization occurs; embryo development (P10); and cone ripening (P11) when seeds mature and later disseminate (Abellanas, 1990; Abellanas and Pardos, 1989; Mutke et al., 2005a). To analyze CN, we considered the period from P1 to P7, when the number of cones is determined. To analyze CW and pine nut weight, we considered the period between P7 and P11, when fruit growth takes place; and to study IS, we considered the period from P1 to P11. Therefore, for each year of measurement and site, the biometeorological variables summarized climatic records of specific periods during the reproductive cycle, comprising 42 months since induction to cone ripening.

Climatic characterization by physio-phenological phases for all sites is presented in Table 3; climatic characterization for each MZ is included as Supplementary material (Tables 1S–3S).

2.3. Fruit production variables

We visited and measured all existing stone pine plantations recorded by INFOR in Chile, aged 8 years and over, which are con-

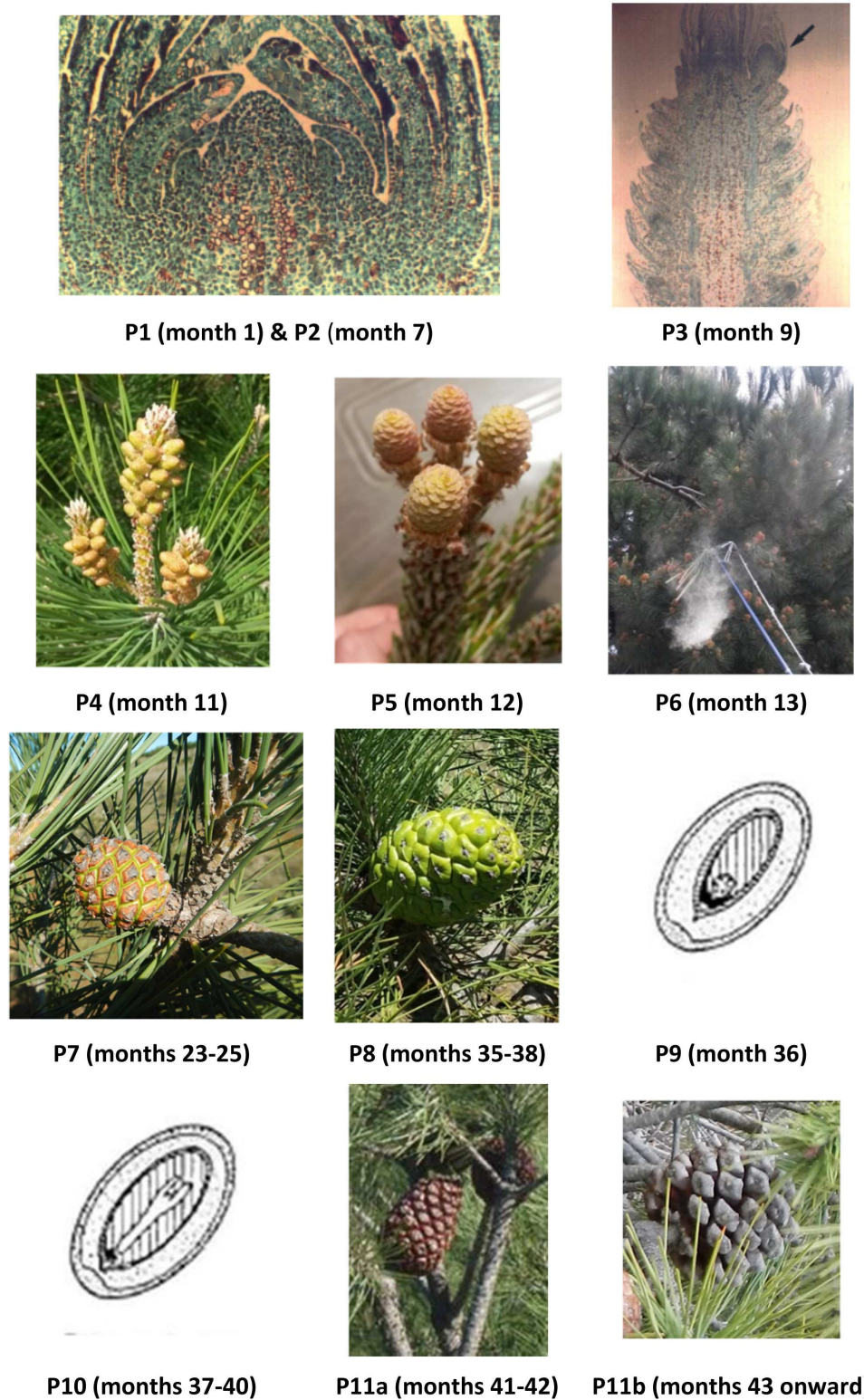


Fig. 2. Stone pine reproductive cycle phases: induction of male primordia (P1) and female primordia (P2); differentiation of reproductive shoots (P3), male flowering (P4), female flowering (P5), pollination (P6), growth of 2 year-old conelet (P7), growth of 3 year-old cone (P8), fecundation (P9), embryo development (P10) and cone ripening (P11a) and seed dissemination (P11b). Pictures of phases P1, P2, P3 were taken from [Abellanas \(1990\)](#); designs were taken from [Abellanas and Pardos \(1989\)](#); other pictures belong to the authors of the present work.

sidered productive in this country ($n=122$). For 3464 stone pine trees distributed in a surveyed area of over 1 million ha, all cones tree^{-1} (CN) were counted from a standing position on the ground (estimation error was determined to be lower than 15%).

For a further detailed analysis of fruit characterization, we identified all superior trees for fruit production (76 individuals located in 46 sites distributed across MZs). Given the high environmental variability and different ages of the base populations, superior

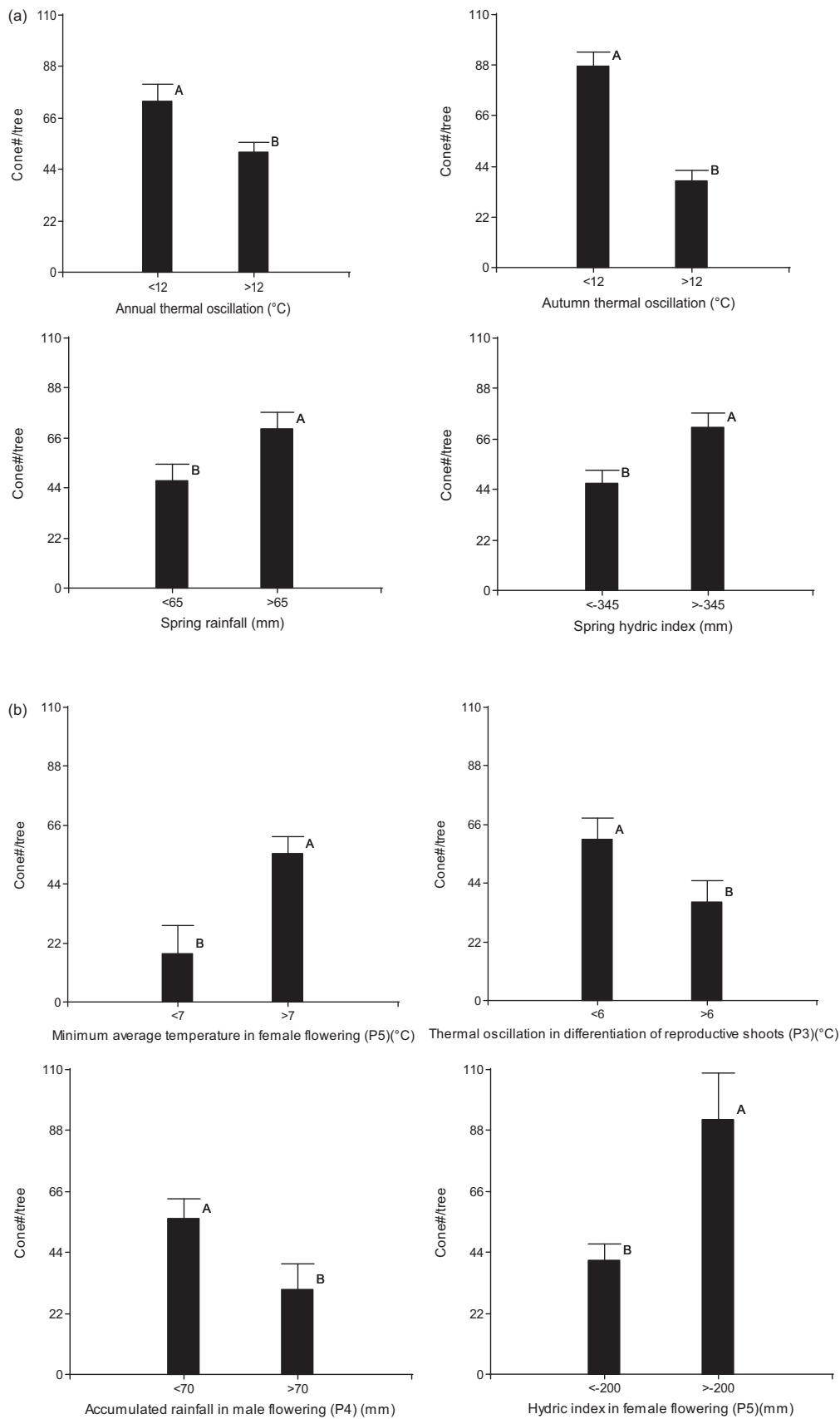


Fig. 3. (a) Climatic variables that influence cone production in Chile. Each threshold was detected by CART analyses. Different letters indicate statistically significant differences ($p < 0.05$). Cone #: cone number; annual thermal oscillation: annual average maximum absolute temperature minus annual average minimum absolute temperature; spring hydric index: spring accumulated rainfall minus spring potential evapotranspiration. (b) Biometeorological variables that influence cone production in Chile. Each threshold was detected by CART analysis. Different letters indicate statistically significant differences ($p < 0.05$). Cone #: cone number; thermal oscillation: average maximum absolute temperature minus average minimum absolute temperature; hydric index: accumulated rainfall minus potential evapotranspiration.

phenotypes were identified by applying the individual valuation method following [Ipinza et al. \(1998\)](#). From each superior tree, a sample of 10 cones was randomly taken, cone weight at harvest (green) (CW) was recorded in the field and in-shell pine nut number cone⁻¹ (IS) as well as other fruit variables (size and weight of in-shell and shelled pine nuts) were measured in the laboratory. The proportion of shelled pine nuts in cones – known as pine nut yield (PNY) –, was calculated by drying the shelled pine nuts to 6% humidity content, weighing them and comparing that value with cone weight at harvest, using the following formula:

$$\text{PNY}(\%) = \frac{\text{Dried shelled pine nut weight}}{\text{Cone weight at harvest (green)}} \times 100$$

Cone productivity (CP) was estimated by considering CN multiplied by CW and by 100, under the assumption that between-tree variability due to competition effects is controlled by plantation management. We estimated a density of 100 trees ha⁻¹ as close to a final density in productive plantations at an adult age (DBH over 30 cm), as indicated by [Mutke et al. \(2012\)](#). Shelled pine nut production (SHP) was calculated based on PNY, also assuming plantations of 100 trees ha⁻¹. As covariates we recorded age and DBH of each tree and presence/absence of water supply.

2.4. Statistical analyses

The relative contribution of climatic and biometeorological variables to productivity measurements was estimated using CART (Classification and Regression Trees) algorithms ([Breiman, 2001](#)). The RT procedure creates a predictive model for a continuous response variable (CN, CW and IS) based on the recurrent classification of the studied cases into groups according to the values (threshold) of the predictor variables (climatic and biometeorological variables). The result of this recursive binary partitioning is a model whose structure can be displayed as a tree-like graph, with each split in the tree labeled according to the variable and threshold used to define the split. Regression trees were used to explain variability of the selected response variables capturing nonlinear relationships and correlations between meteorological variables. The algorithm was not applied on productive variables showing low variability (CV < 20%) or strongly correlated to the selected dependent variables. RT have successfully been used to model growth and yield from highly correlated climatic variables ([Thuiller et al., 2003](#); [Lobell et al., 2005](#); [Heredia et al., 2010](#)).

A total of eight RTs, four using climatic variables (in all sites and by MZ) and four using biometeorological variables (in all sites and by MZ) as predictors were built for each of the stone pine productive variables. Boosting ([Elith et al., 2008](#)) was used as a validation tool; only the first two nodes of each RT were used to identify the predictors that most strongly influenced the response variables. As confirmatory analysis we performed a non-parametric ANOVA to evaluate statistical significance of differences between yield mean groups suggested by the thresholds of the first RT node (n > 15). All ANOVAs included tree age and macrozone effects as controlling variables. We used the same non-parametric approach to evaluate water supply effects on cone production. The relationship between DBH and cone production was analyzed using a linear regression model. The analyses were performed using the software INFOSTAT and its interface with the software R ([Di Rienzo et al., 2013](#)).

3. Results

3.1. Fruit productivity in each stone pine macrozone in Chile

The description of stone pine cone productivity for all studied sites and per macrozone (MZ) is presented in [Table 4](#). Average cone number tree⁻¹ (CN), cone weight at harvest (CW) and in-shell pine

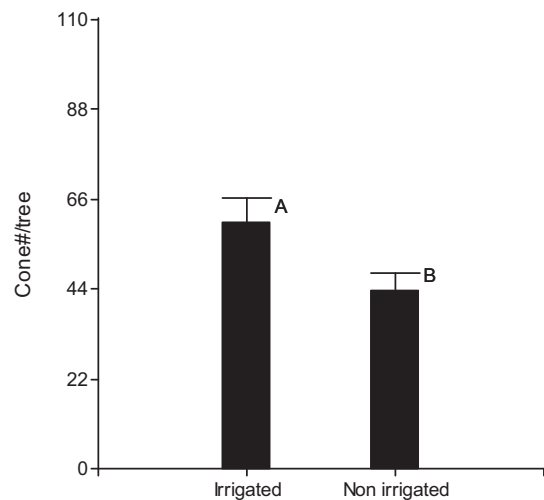


Fig. 4. Water supply effect on cone production using data from all sites. Different letters indicate statistically significant differences ($p < 0.05$).

nut number per cone (IS) across sites were 57 cones tree⁻¹, 495 g and 100 in-shell pine nuts cone⁻¹, respectively, being the first two higher in the south. Pine nut yield (PNY) was in average 3.9%, with 3.5% in Dry Coast, 3.7% in the North MZ and 4.3% in the South MZ. In-shell nut weight (ISW) was the highest in the South MZ. The lowest value of shelled pine nut weight (SHW) was recorded in the Dry Coast MZ. Average CP reached 2821 kg 100 trees⁻¹, increasing from north (2355 kg 100 trees⁻¹) to south (3183 kg 100 trees⁻¹); similarly, average shelled pine nut production amounted to 110 kg 100 trees⁻¹ across the country, increasing from north (87 kg 100 trees⁻¹) to south (137 kg 100 trees⁻¹).

3.2. Fruit productivity and climate

3.2.1. Cone number tree⁻¹ (CN)

The climatic variables that significantly influenced CN were annual and autumn thermal oscillation, spring rainfall and water deficit ([Fig. 3a](#)). Accordingly, we detected three key physio-phenological phases that affected CN: differentiation of reproductive shoots (P3), and male (P4) and female flowering (P5), which were favored by a thermal oscillation below 6 °C in P3, rainfall below 70 mm in P4, and minimum temperature above 7 °C and a low water deficit in P5 ([Fig. 3b](#)).

Regression trees showed that CN ([Fig. 1a](#) in the Supplementary material) was influenced by autumn thermal oscillation, with CN decreasing at ranges greater than 11.8 °C and averages of 80 and 40 cones tree⁻¹ below and above that threshold. In sites with narrower autumn thermal oscillation, those with spring minimum temperature below 7.3 °C presented a superior number of cones tree⁻¹ (154 vs 68). With autumn thermal oscillation above 11.8 °C and summer maximum temperatures above 27.4 °C, CN increased under a low spring water deficit (68 vs 41).

An average minimum temperature above 6.9 °C during P5 favored CN (60 vs 20) ([Fig. 1b](#) in the Supplementary material). On the other hand, when that minimum temperature was exceeded, accumulated rainfall of above 71.6 mm in P4 had a negative effect on CN (37 vs 75).

Besides being correlated with climatic variables, CN was significantly related to DBH and water supply. DBH was linearly related to CN, suggesting that for every cm of DBH growth, an increase in CN of half a cone can be expected ($CN = 19.7 + 0.45 \times DBH$, $n = 118$; $p = 0.0066$). Statistically significant differences between irrigated and non-irrigated plantations were found for CN (60 vs 44 cones

Table 4
Characteristics of fruit production per stone pine macrozones in Chile.

Production Variables	North MZ	Dry Coast MZ	South MZ	All sites
Cone tree ⁻¹ (#) (CN)	49 (111)	59 (150)	62 (122)	57 (126)
Weight of cone at harvest (green) (g) (CW)	480.7 (27)	489.5 (17)	513.4 (22)	495.0 (23)
Cone length (cm) (CL)	10.7 (17)	11.2 (14)	12.1 (18)	11.3 (18)
In-shell pine nut cone ⁻¹ (#) (IS)	93 (28)	107 (20)	106 (16)	100 (23)
Shelled pine nuts cone ⁻¹ (#) (SH)	87 (31)	94 (28)	101 (19)	94 (26)
In-shell pine nut weight (g) (ISW)	0.9 (16)	0.9 (19)	1.0 (13)	0.9 (15)
Shelled pine nut weight (g) (SHW)	0.22 (19)	0.18 (17)	0.21 (15)	0.21 (18)
Cone to shelled pine nut yield (%) (PNY)	3.7 (26)	3.5 (28)	4.3 (18)	3.9 (24)
Cone productivity (kg 100 trees ⁻¹) (CP)	2355 (96)	2888 (190)	3183 (159)	2821 (155)
Shelled pine nut productivity (kg 100 trees ⁻¹) (SHP)	87 (91)	101 (196)	137 (172)	110 (154)

Values in parentheses correspond to coefficient of variation (in percentage). n = 46 for all variables, with the exception of CN (n = 122). # = number. Mean values are adjusted by tree age.

Table 5
Main climate variables that showed a significant influence on stone pine cone production, cone weight and quantity of in-shell pine nut per cone in Chile.

Dependent variable	Autumn maximum temperature (MXTau)	Annual average temperature (AT)	Rainfall (PP)	Spring rainfall (PPsp)	Hydric index ^a (HI)	Spring hydric index (HIsp)	Thermal oscillation ^b (TO)	Autumn thermal oscillation (TOau)
Cone number tree ⁻¹ (CN)				≥65 mm (46%)		≥-345 mm (60%)	<12 °C (43%)	<12 °C (125%)
Cone weight (CW)		≥14 °C (38%)	≥507 mm (29%)		≥-914 mm (27%)			
In-shell pine nut number cone ⁻¹ (IS)	≥19 °C (18%)				≥-914 mm (37%)			

Values in parentheses correspond to the expected increase of the dependent variable under the identified key climatic conditions.

^a Hydric index was calculated as accumulated rainfall in the period minus potential evapotranspiration of the same period; for the spring hydric index, spring data were considered.

^b Thermal oscillation: average maximum absolute temperature, minus average minimum absolute temperature; for the autumn thermal oscillation, autumn data were considered.

tree⁻¹), suggesting an increase of over 25% of tree cone production associated with this practice (Fig. 4).

In the analysis focused on MZ, the variables related to temperature were also the main climatic variables affecting CN; autumn thermal oscillation (TOau) was the most relevant factor in North MZ, increasing CN in sites where it was below 11.6 °C (105 vs 38). Low water deficit (less than 332 mm) during induction of male primordia (P1) was found to favor CN. In the Dry Coast MZ, CN was negatively influenced by maximum autumn temperature above 17.9 °C (105 vs 26). In the South MZ, sites with spring minimum average temperature below 6.9 °C had greater fruit production (116 vs 50). CN was favored by a thermal oscillation below 6.2 °C at differentiation of reproductive shoots (P3) (93 vs 38).

3.2.2. Cone weight (CW)

The climatic variables that significantly influenced CW along the climatic gradient in Chile were annual average temperature, annual water deficit and annual rainfall, and according to physio-phenological phases, maximum average temperature and water deficit during embryo development (P10), and accumulated rainfall in 2 year-old conelet growth (P7) (Fig. 5).

The variable that best explained CW was annual average temperature (AT). Sites with higher AT (>14.1 °C) had a higher CW (438 vs 549 g), whereas in sites with AT smaller than <14.1 °C, CW was favored (334 vs 461 g) by a decrease of water deficit (Fig. 2aS in the Supplementary material). The analysis focusing on physio-phenological phases also evidenced the importance of temperature, showing that CW was favored by maximum temperature above 23.2 °C during P10 (403 vs 519 g) and by water deficit during P10

(spring-autumn) below 774 mm (404 vs 568 g) (Fig. 2bS in the Supplementary material).

Considering macrozones, we observed the effect of annual rainfall in the North MZ and of annual average temperature in the Dry Coast and South MZs. In the North MZ, sites with annual rainfall above 507 mm produced cones of 660 g, whereas below that threshold, CW decreased by nearly 35%. Below 507 mm, a winter average temperature above 8.3 °C favored CW. Rainfall over 14.3 mm during growth of 2 year-old cones represented a CW increase of over 35% (600 vs 419 g), as well as an average temperature in P8 below 13.9 °C (631 vs 396 g). In the Dry Coast MZ, when average temperature was above 14.2 °C, CW was 585 g, whereas at lower average temperature values it decreased approximately by 25%. Accumulated rainfall during 2 year-old conelet growth (P7) at above 14.3 °C contributed to production of heavier cones (660 vs 419 g). In the South MZ, where water is not generally a limiting factor for stone pine growth, annual average temperatures above 12.3 °C produced heavier cones (512 vs 368 g), and with minimum annual temperature below 7.6 °C, cones had greater weight (586 vs 472 g). In the analysis focused on physio-phenological phases, we observed the positive effect of a maximum temperature above 22.5 °C on CW (514 vs 385 g) during embryo development (P10).

3.2.3. In-shell pine nut number (IS)

Climatic variables that significantly influenced IS across Chile were annual water deficit and autumn maximum temperature; and accumulated rainfall during induction of male primordia (P1); maximum average temperature during 2 year-old conelet growth (P7), and accumulated rainfall during 3 year-old cone growth (P8)

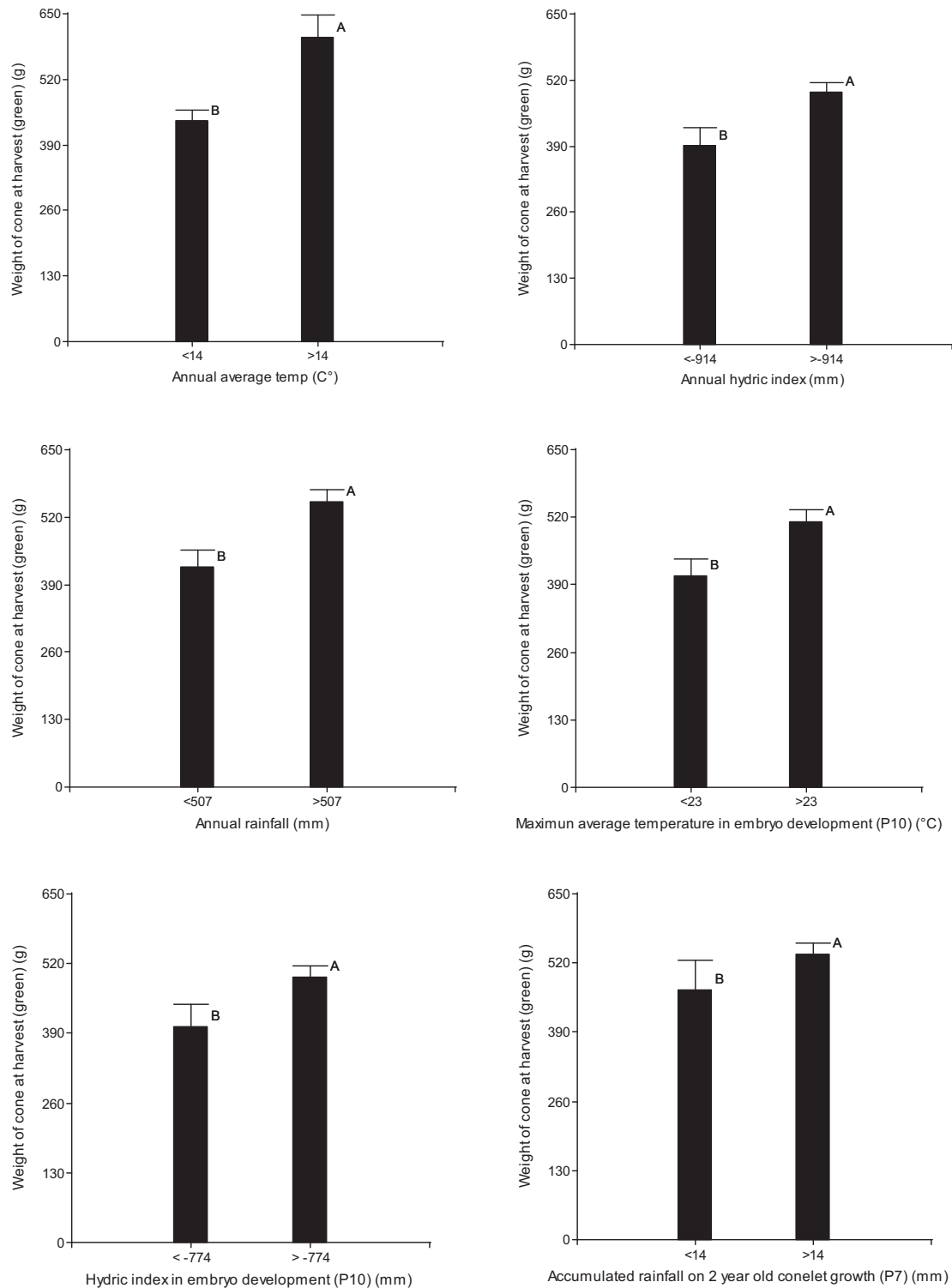


Fig. 5. Variables that influence cone weight in Chile. Each threshold was detected by CART analysis. Different letters indicate statistically significant differences ($p < 0.05$). Annual hydric index: annual rainfall minus annual potential evapotranspiration.

and cone ripening (P11) (Fig. 6). Hydric index (HI) was the variable that best explained IS. Sites with water deficit below 914 mm had a higher IS value (108 vs 79) than sites with water deficit above that value (Fig. 3aS in the Supplementary material). The analysis focused on physio-phenological phases also evidenced the importance of water availability, showing a positive effect of accumulated rainfall of over 133 mm on IS (111 vs 91) during cone ripening (P11) (Fig. 3bS in the Supplementary material).

The analysis focused on MZ detected that in the North MZ, IS was significantly greater with water deficit below 914 mm (109 vs 79) and maximum average temperature during induction of male primordia (P1) below 27 °C (109 vs 79). In the Dry Coast MZ, when autumn maximum temperature was below 19.1 °C, IS reached 116, whereas at higher values, IS decreased over 25%. The analysis of the effect of bioclimatic variables on IS considering physio-phenological phases in this MZ showed that maximum tem-

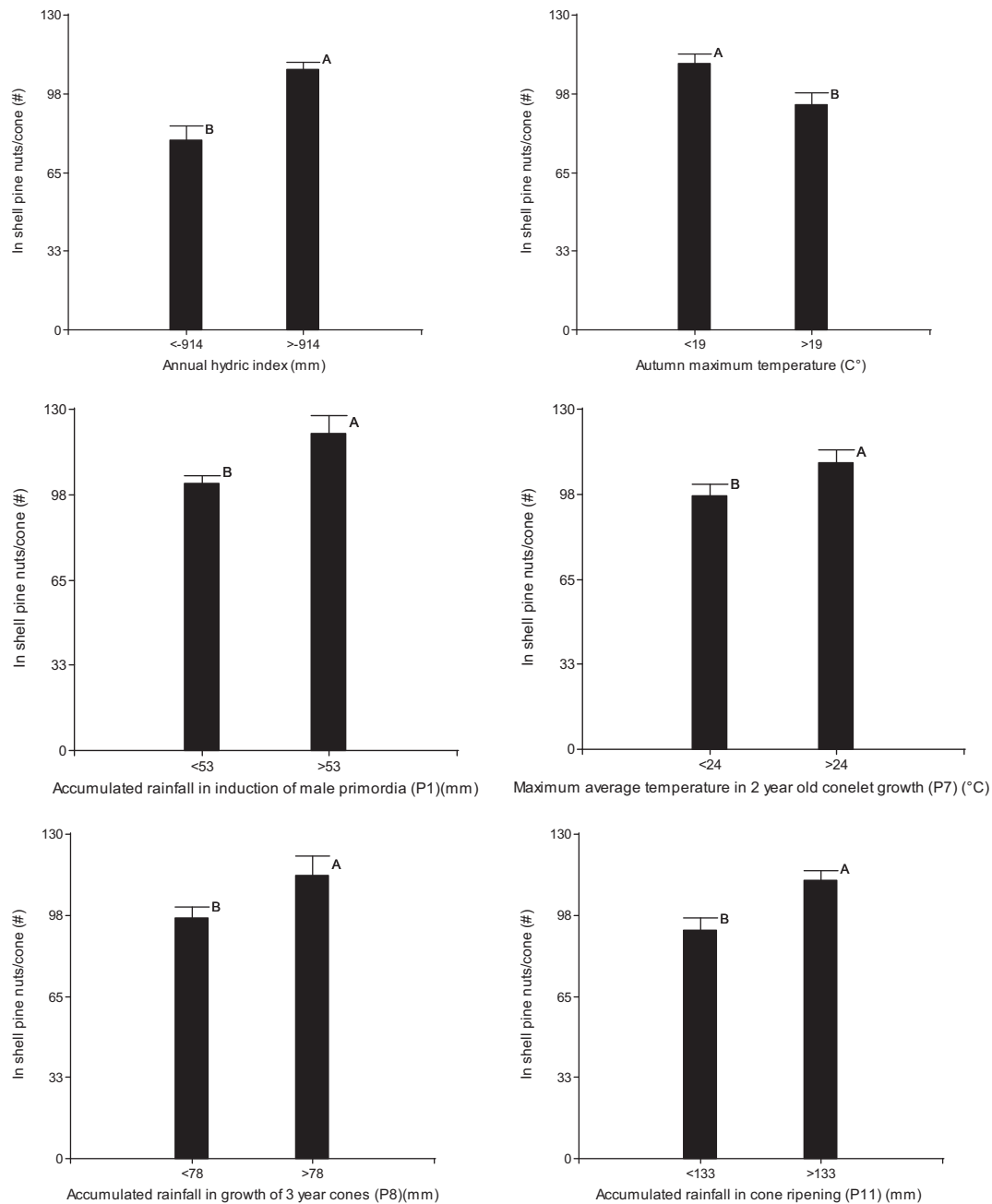


Fig. 6. Variables that influence in-shell pine nut number per cone in Chile. Each threshold was detected by CART analysis. Different letters indicate statistically significant differences ($p < 0.05$). #: number; annual hydric index: annual rainfall minus annual potential evapotranspiration.

perature above 23.8 °C during 2 year-old conelet growth (P7) had a positive influence of over 27%. In the South MZ, when minimum summer temperature was above 12 °C, IS reached 136, whereas at lower values, IS decreased to 105. In this MZ, accumulated rainfall during 3 year-old cone growth (P8) above 78.4 mm also favored IS (116 vs 93), as well as accumulated rainfall during induction of male primordia (P1) of above 52.4 mm (127 vs 109).

Tables 5 and 6 summarize the results regarding the influence of climatic and biometeorological variables on CN, CW and IS based upon the complete material from Chile.

4. Discussion

This study has shown the relevance of climatic variables for stone pine fruit productivity, with increasing values along macro-

zones from north to south. Even though fruit productivity was different along the climatic gradient in Chile, all studied variables showed interesting values when compared with the native range of the species. The average cone production in Chile, of 57 cones tree⁻¹, represents a yield of 28 kg tree⁻¹, which is higher than data from its native habitat and lower than values reported for Lebanon (40 kg tree⁻¹) (Sfeir, 2011).

In Spain, stone pine production was found to be dependent upon climatic conditions (Gordo, 2004; Mutke et al., 2005a), with production being related to rainfall and temperature during the earliest cone development phases. Our results showed that high spring rainfall and small thermal oscillation had a high positive effect on cone number tree⁻¹ (CN). Regarding temperature, we observed that autumn thermal oscillation smaller than 12 °C favored cone production, precisely when induction of female primordia occurs. On

Table 6Main biometeorological variables that showed a significant influence on stone pine cone production, cone weight and quantity of in-shell pine nut per cone in Chile^a.

Phase	Induction	Differentiation	Flowering		Cone Development			
	Male primordia	Reproductive shoots	Male	Female	Growth of 2 year-old conelet	Growth of 3 year-old cone	Embryo development	Cone ripening
Year	P1	P3	P4	P5	P7	P8	P10	P11
Date	0		1		2		3	
From	Nov., 15	July, 15	Sep., 15	Oct., 15	Sep., 15	Sep., 15	Nov., 15	Mar., 15
To	Jan., 15	Sep., 15	Nov., 15	Dec., 15	Jan., 15	Feb., 15	Apr., 15	June, 15
Cone number tree ⁻¹ (CN)		Thermal oscillation ≤ 6°C (65%)	Rainfall ≤70mm (87%)	Min. temp ≥ 7°C (205%) Hydric index [†] ≥-200mm (130%)				
Cone weight (CW)					Rainfall > 14 mm (14%)		Max. temp ≥ 23°C (26%) Hydric index >-774 mm (23%)	
In-shell pine nut number cone ⁻¹ (IS)	Rainfall >53mm (19%)				Max. temp ≥ 24°C (12%)	Rainfall > 78mm (18%)		Rainfall >133 mm (22%)

Values in parentheses correspond to the expected increase of the dependent variable under the identified key biometeorological conditions.

^a Hydric index was calculated as accumulated rainfall in the period minus potential evapotranspiration of the same period.

the other hand, spring minimum temperature above 7 °C had a positive effect on fruiting, when both male and female flowering and pollination take place.

Thermal fluctuations have been reported to influence cone initiation in several ways: by increasing cone differentiation when temperature is below average (Forcella, 1978) or accelerating it with increasing temperature (Lester, 1967). Accordingly, we found a negative effect of thermal oscillation greater than 6 °C on CN at reproductive shoot differentiation (P3).

Higher than average temperatures during seed cone initiation in *P. ponderosa* Dougl. ex Laws. have been associated with above-average cone production (Krannitz and Duralia, 2004); this effect was also demonstrated in other *Pinus* species, such as *P. sylvestris* L. (Karlsson, 2000). In our study, this relationship was observed in the Dry Coast MZ, where minimum average temperature above 12 °C during induction of male primordia (P1) significantly favored cone production.

Other fruit species have been found to be negatively affected by the lack of chilling, with different consequences, such as delayed flowering, extended flowering period, weak vegetative growth and high heterogeneity in fruit size (Ghrab et al., 2014). To our knowledge, this aspect has not been studied in stone pine; hence, we suggest addressing this issue in future studies, because we assume that this Mediterranean species may have such requirement. Elucidating this aspect would help to further define appropriate areas for the species cultivation for fruit production under climate change, which would cause temperature increases and thermal oscillation decreases (Martelo, 2004; Del Río, 2005).

However, expected rainfall decreases would have a negative impact on the species' productivity. In fact, Fontes et al. (2013) reported that cone production depends highly and positively on accumulated rainfall in winter and spring, before the onset of pollination. Mutke et al. (2005a) found rainfall to be determinant for cone productivity at certain key periods during the 4-year-old cone development period. According to these authors, cone yield was favored by high water availability at the time of primordia formation, pollination and growth of 3-year-old cones up to cone ripening. High rainfall during flowering promotes high cone production (UNAC, 2014), and Calama et al. (2007) also reported a

positive effect of spring rainfall on female flowering and derived cone production. We quantified the effect of rainfall and water deficit on CN, with both variables confirming a positive relationship between CN and spring water availability. However, we also found a negative effect of high accumulated rainfall (>70 mm) during male flowering (P4). This finding is in agreement with records of Parlak et al. (2013), who pointed out the importance of the pollination period – influenced by altitude, rainfall, high relative humidity and extreme temperatures – on cone production. These authors found that non-productive areas located below 500 m a.s.l. were characterized by a thermal oscillation of 22 °C and more frequent days with temperature below 10 °C, early and late frosts, high relative humidity and fog.

Our results confirmed that rainfall and temperature were important climatic variables for stone pine fruiting across Chile. However, their relative importance varied among growth MZs, and this was observed for all fruit traits analyzed in this study. The highest fruit traits were recorded in the South MZ, where the highest vegetative growth was also observed (Loewe et al., 2015). Here, gains in cone productivity reached 35% with respect to the North MZ.

Since annual rainfall and temperature fluctuations can induce changes during the cone induction period, more than one phenological calendar in the area cultivated with stone pine in Chile might be used for future studies.

Besides climate, management may also influence primordia induction. The fact that irrigation had a significant effect on stone pine cone production, which is not in agreement with Aleta and Vilanova (2014), could be partially explained by the findings of Nilsson and Wiklund (1992), who reported dry mass increases due to irrigation. In that work, irrigation resulted in faster increment of needle dry mass because of an increased formation of needles and a reduced shedding of older ones.

In Catalonia, an irrigation test was established in 2010 to study the effect of different water regimes on cone induction and production (Bono and Aleta, 2011). For the 2014 production Aleta (2014, pers. comm.) reported 18 and 23 strobili, conelets and cones per tree without and with irrigation, respectively, a difference of over 25% on average. In our study, similar differences in productivity

were observed between irrigated and non-irrigated plantations due to the reported significant effect of irrigation on cone number.

Irrigation also results in increased DBH growth rates (Loewe et al., 2015). Accordingly, we found a significant relationship between cone production and DBH. This is consistent with findings in *P. ponderosa* reported by Krannitz and Duralia (2004), who stated that tree diameter was a better predictor of cone production than age, and that trees of larger diameter also produced cones more frequently. Crown variables are also closely associated with cone production in *P. pinea* according to Correia and Freire (2014), but those variables were not considered in this study.

Cone quality is expressed through cone weight, which is assumed to control factors such as yield, empty/damaged pine nuts and pine nut size (Calama et al., 2007), varying from 50 to 800 g in Europe, and similarly in Chile (105–935 g cone⁻¹). According to these authors, weight can even determine the price paid per cone in the nut industry; in fact, heavier cones (up to 350 g) show higher yield in pine nuts and produce larger pine nuts, both shelled and in-shell. Furthermore, they indicate that even the rate of empty/damaged pine nuts is smaller in heavier cones.

Mutke (2005) indicates that stone pine cones are usually about 250–350 g in weight, but weight can vary between 200 and 500 g (Mutke et al., 2005a). In Tunisia, average cone weight is 252 g cone⁻¹ (Schröder et al., 2014); in Portugal, this value ranges between 256 and 280 g cone⁻¹ (Gonçalves and Pommerening, 2012), and in Chile we found an average of 495 g cone⁻¹, with a low variability expressed as coefficient of variation equal to 23%.

A significant year effect on cone weight caused by climate has been reported (Calama et al., 2008a). Our results showed that annual rainfall and annual water deficit significantly affected cone weight at harvest (CW), which could make these variables useful indicators for irrigation practices. In particular, we found that annual rainfall higher than 507 mm significantly increased CW, which is in agreement with several works, such as that of Mutke et al. (2006), who reported CW lower than 200 g with annual rainfall below 400 mm. Fontes et al. (2013) also reported a high dependence of cone production on water deficit, a great effect of late spring-summer rainfall on weight and size of pine nuts and cones; and Calama et al. (2007) observed that CW of the next crop is largely affected by summer to winter rainfall. We found that accumulated rainfall during 2 year-old conelet growth (P7) significantly influenced CW and that water deficit below 774 mm during embryo development (P10) increased CW by almost 30%. We also observed a significant effect of temperature during P10, when maximum temperatures above 23 °C increased CW by over 20%.

We found that in-shell pine nut number per cone (IS) was positively benefited by an autumn maximum temperature below 19 °C, but negatively affected by high water deficit (above 914 mm). We did not find any reference on the dependence of this variable on climatic factors. However, it has been established that IS is highly variable, depending upon production and cone size (Piqué, 2004). We observed that a small thermal oscillation favors cone production and that water availability is positive for CW; therefore, these variables are also expected to affect IS.

The fruit productivity variables CN and IS increased from north to south in Chile. Therefore, the average CP, estimated in 28 kg tree⁻¹, would also follow the same pattern along with an increase in annual rainfall. This assumption is in agreement with findings of Yagüe (1994), who found that in mature forests in Spain, productivity ranges between 54 and 325 kg ha⁻¹ with rainfall of 350–450 mm year⁻¹, and 113–433 kg ha⁻¹ with 700–800 mm year⁻¹. With 100 trees ha⁻¹ in Chile, which is a lower density than in the average Spain forests (Borrero, 2004), we would expect increasing cone production (CP) from 2355 to 3183 kg 100 tree⁻¹, and shelled pine nut production (SHP) from 87 to 137 kg 100 ha⁻¹ from north to south, where annual rainfall increases from

383 to 1047 mm year⁻¹. Such increases represent gains of 35% in CP and 57% in SHP. In Italy, CP values ranging between 500 and 1500 kg ha⁻¹ were reported (Crawford, 1995); in Portugal, CP reached 700–900, and up to 2000 kg ha⁻¹; in Tunisia, Schröder et al. (2014) reported an average productivity of 1599 kg ha⁻¹, and in Argentina a production of 2700 kg ha⁻¹ was reported by Ottone (1989). Even though the studied plantations were non-fertilized, our results suggest that the potential fruit productivity in Chile is high under favorable climate conditions, as those in the south. However, further studies focusing on the interaction of climatic influence with soil conditions, fertilization and other agronomic management practices are recommended in order to improve the species intensive cropping.

5. Conclusions

Tree cone production and cone productivity of stone pine showed marked differences along the climatic gradient in Chile, increasing from north to south. The lowest in-shell pine nut number cone⁻¹ was found in the North macrozone, while the lowest cone to shelled pine nut yield in the Dry Coast macrozone. For cone number, the most relevant climatic variables explaining fruit productivity were spring rainfall and spring hydric index. Accordingly, minimum average temperature and hydric index affected female flowering, accumulated rainfall affected male flowering, and thermal oscillation influenced differentiation of reproductive shoots. Cone weight at harvest and in-shell pine nut number cone⁻¹ increased with a low annual water deficit.

As practical applications of our results, we determined that a good selection of sites for fruiting of the species in Chile should ensure spring minimum average temperature above 7 °C; annual and autumn thermal oscillation lower than 12 °C; and a high spring rainfall, except during the male flowering period. Water supply proved to be a significant management practice for individual cone production (over 25% higher than in non-irrigated plantations). Moreover, in light of climate change, we consider that it represents a mitigation management practice to enhance fruiting, with requirements depending upon local water deficit. Further studies are needed to interpret these findings in relation to soil and other agronomic management practices.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.04.011>.

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